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Causes for Morphological Variation among Populations of Herring *Clupea pallasii* in the Far Eastern Waters*1

Yasuji Kanno*2

(Received July 16, 1988)

Geographic and environmental causes of variations in meristic and morphometric characters were examined for the ten herring populations in the Far Eastern waters. A study of the correlations between the characters of each population and the latitude, salinity and water temperature at the spawning grounds showed that five characters of initial growth, upper gill rakers, lower gill rakers, head length-body length relation and predorsal length-body length relation are closely related to the latitude or water temperature, but showed no relation with the salinity in the spawning grounds.

Three factors were extracted by factor analysis for the ten morphological characters in populations. One of them which seems to have no correlation with the three environmental properties examined is the factor suggesting genetic differences between the populations. The variations in morphological characteristics may be associated with each population's ecological, adaptitional and quantitative properties during their evolutional courses in the Pacific Ocean.

The author, in his studies[1,2] up to this point, reported that there are ecological and morphological variations among the herring populations distributed in Far Eastern waters. Such variations among populations are not only important as characteristics to distinguish resource-oriented genealogical groups, but are thought to be closely related to long-term population dynamics in connection with natural selection and the adaptation of populations which operate in the process of change of characters. In this study, the fact will be discussed that the principal causes of morphological variation among herring populations are the water temperature and latitude of the spawning grounds, and the presence of a genetic variation among populations whose correlation with the environment is

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unclear will be conjectured as the next leading cause. Also, the relationship between the variation among herring populations and quantitative fluctuations will be considered.

Materials and method

As the materials, samples collected from the ten populations representing the herring distribution region in Far Eastern waters were used. The conditions of collection and method of measurement of these samples were explained in detail in KANNO.[1,2] In this report, using initial growth and the two types of morphological characters described below, specifically the sample means of four meristic characters and the adjusted means of morphometric lines with respect to five morphometric characters pertaining to body part lengths and body weight to body length, the geographic variations in the characters was analyzed. With respect to these morphological characters, the variations among populations have been statistically made clear.[2] Also, by factor analysis[3,4] using the same data, a contraction of variation with respect to multiple characters was done. The data used in the analysis and their abbreviations are as follows.

Initial growth (IGR): Standard body length when the first annual ring has formed on scales

Number of anal fin rays (AF): Number of anal fin rays perfectly ramified at the base

Number of vertebrae (VN): Total number of vertebrae including caudal cylindrical bones

Number of upper gill rakers (UGR): Total number of perfectly formed upper gill rakers

Number of lower gill rakers (LGR): Total number of perfectly formed lower gill rakers

Body weight - body length relationship (BW/BL): Adjusted mean of morphometric line of body weight to body length

Preanal length - body length relationship (PAL/BL): Adjusted mean of morphometric line of preanal length to body length

Head length - body length relationship (HL/BL): Adjusted mean of morphometric line of head length to body length

Predorsal length - body length relationship (PD/BL): Adjusted mean of morphometric line of predorsal length to body length

Prepelvic length - body length relationship (PP/BL): Adjusted mean of morphometric line of prepelvic length to body length (442)

Results

Geographic variation in characters. The means or adjusted means of each character relative to the latitude where the spawning grounds of each population are located are compared in Fig. 1. Also, the rank correlation coefficients

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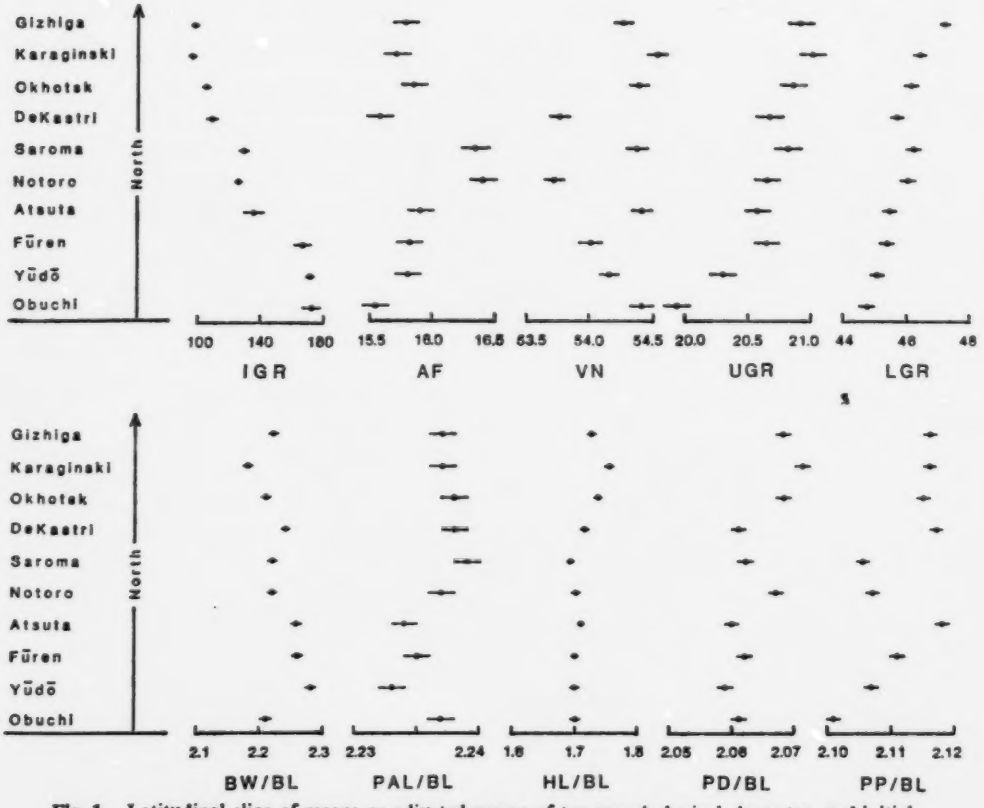

Fig. 1. Latitudinal cline of means or adjusted means of ten morphological characters and initial growth of body length, means and standard errors are shown by solid circles and horizontal lines. Notations are in text.

Table 1. Spearman's rank correlation coefficients between morphological or ecological characters, and three physical condistions

Character	Latitude	Salinity	Temperature
IGR*1	−0.976*2	−0.414	0.437
AF	−0.006	0.306	0.247
VN	0.079	0.126	−0.665*3
UGR	0.964*2	0.469	−0.310
LGR	0.939*2	0.487	−0.304
BW/BL	−0.427	0.414	0.373
PAL/BL	0.521	0.055	0.030
HL/BL	0.758*2	0.180	−0.716*2
PD/BL	0.771*2	−0.266	−0.249
PP/BL	0.531	0.609	−0.657*3

*1 Growth of body length in the first year of life.
*2 Significant at 1% level.
*3 Significant at 5% level.

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vis-a-vis the latitude of the spawning grounds and the salinity and water temperature in the spawning season of each population, as well as the results of a regressionless hypothesis test on non-correlation are shown in Table 1. Note that in the case of Okhotsk, Karaginski and Gizhiga Bay, data on the salinity of the spawning grounds could not be obtained, so they were excluded from the calculation of the correlation coefficients involving this element. The results analyzed with respect to each character are as follows.

IGR: The initial growth of 17 cm at Obuchi Marsh and Yudo Marsh is the highest and 9.6 cm at Karaginski is the lowest. A clear geographic tendency to be high in the south and low in the north can be discerned throughout all waters. The rank correlation coefficients vis-a-vis latitude, salinity and water temperature were -0.976, -0.414 and 0.437, respectively, with the negative correlation with the latitude of the spawning ground being significant.

AF: Looking at the six populations around Japan, a low value can be seen in the population of Obuchi Marsh located most southerly and high values in Notoro Lake and Saroma Lake. Consequently, as far as the six populations around Japan are concerned, a tendency to be low in the south and high in the north (443) can be seen, but if the four populations in the northern waters are added in, these all indicate values below the middle, so as a whole the tendency for the

values to increase with latitude cannot be seen. The rank correlation coefficients vis-a-vis latitude, salinity and water temperature were -0.006, 0.306 and 0.247, respectively, with none being significant.

VN: High values can be seen in the populations of Okhotsk, Karaginski, Gizhiga Bay and Obuchi Marsh, Furen Lake, Saroma Lake, and low values in Notoro Lake and DeKastri. Looking at the four populations in the northern waters, a tendency to be low in the south and high in the north can be seen, but in the six populations around Japan low values and high values are intermingled, and throughout the whole no straight-line tendency can be seen. The rank correlation coefficients relative to latitude, salinity and water temperature were 0.079, 0.126 and -0.665, respectively, with the negative correlation with water temperature being significant.

UGR and LGR: Both the upper gill rakers and lower gill rakers have a pronounced tendency to be low in the south and high in the north. In the six populations around Japan and the four populations in northern waters, the position of the trend line differs. The rank correlation coefficient relative to latitude is significant ($P < 0.001$) for both the upper (0.964) and lower gill rakers (0.939). The correlations with the salinity and water temperature of the spawning grounds do not indicate significance for either character.

BW/BL: Looking at the values of the adjusted means for both sexes lumped together in terms of the relationship with latitude, collectively a tendency to be high in the south (Yudo Marsh 2.278) and low in the north (Karaginski 2.179) is shown. However, the variation among populations is large, and the rank correlation coefficients relative to latitude (-0.427), salinity (0.414) and water temperature (0.373) do not indicate significance.

PAL/BL: Because the adjusted means for the four populations in the northern waters are high, as a whole a tendency to be low in the south and high in the north is shown. However, the variation among populations is large, and

among the six populations around Japan are the maximum value (Saroma Lake 2.239) and minimum value (Yudo Marsh 2.233). The rank correlation coefficients relative to latitude (0.521), salinity (0.055) and water temperature (0.030) are all not significant.

HL/BL: The values of the adjusted means show a straight-line tendency to be low in the south and high in the north. The rank correlation coefficients are significant relative to latitude (0.758) and water temperature (-0.716) but not significant with salinity (0.180).

PD/BL: The values of the adjusted means show a straight-line tendency to be low in the south and high in the north. The rank correlation coefficient is significant relative to latitude (0.771) but not significant with salinity (-0.266) and water temperature (-0.249).

PP/BL: Collectively a tendency to be low in the south and high in the north is seen. However, among the six populations around Japan are the maximum value (Atsuta 2.118) and minimum value (Obuchi Marsh 2.101), and the variation among populations is large. The rank correlation coefficients relative to latitude, salinity and water temperature were 0.531, 0.609 and -0.657, respectively, with the negative correlation with water temperature being significant.

Summary: The initial growth (IGR) showed a pronounced tendency to be high in the south and low in the north. In terms of the meristic characters, UGR and LGR showed a significant correlation with latitude and VN with water temperature, respectively, indicating a close connection with the two elements. In terms of the morphometric characters, BW/BL shows a variation of being high in the south and low in the north, while PAL/BL, HL/BL, PD/BL and PP/BL change in the opposite direction to this. Particularly with the three characters HL/BL, PD/BL and PP/BL, the connection with the two elements is strong. None of the characters indicates a strong correlation with salinity.

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Looking at the connection among populations throughout all the characters, the three populations of Okhotsk, Karaginski and Gizhiga Bay in the northern waters take on similar values with all characters and the positions they occupy among all the populations bear a close resemblance, whereas with the six populations around Japan the variation for each character is large, and for the three characters AF, PAL/BL and PP/BL they show the maximum value and minimum value among all populations. Also, with the other characters excluding IGR and (444)

Table 2. Eigenvalues and cumulative contribution (%) of variance calculated by principal component analysis from the correlation matrix of ten morphological characters

Factor	Eigen value	Cumulative percent
1	5.157	51.6
2	1.676	68.3
3	1.497	83.3
4	0.792	91.2
5	0.476	96.0

Table 3. Factor loadings computed by varimax method of factor analysis for ten morphological and ecological characters. Notations are in text

Character	f_1	f_2	f_3
IGR	−0.843	−0.463	−0.008
AF	−0.021	0.274	0.827
VN	−0.051	0.311	−0.667
UGR	0.877	0.287	0.227
LGR	0.765	0.456	0.212
BW/BL	−0.219	−0.916	0.251
PAL/BL	0.146	0.822	0.157
HL/BL	0.749	0.317	−0.522
PD/BL	0.610	0.658	−0.112
PP/BL	0.912	−0.253	−0.200

Table 4. Estimated factor scores computed by factor analysis for ten populations

Locality	f_1	f_2	f_3
Obuchi	−2.145	0.716	−1.317
Yūdō	−0.776	−1.479	−0.046
Fūren	−0.177	−1.007	0.328
Atsuta	0.346	−1.283	−0.343
Notoro	−0.137	0.632	1.851
Saroma	−0.598	1.138	1.248
DeKastri	0.605	−0.651	0.198
Okhotsk	0.671	0.657	−0.559
Karaginski	1.046	1.009	−1.304
Gizhiga	1.165	0.270	−0.055

Table 5. Speaman's rank correlation coefficients between varimax rotated factor score and three physical conditions

Factor	Latitude	Salinity	Temperature	Related character
f_1	0.915*1	0.541	−0.627*2	IGR, UGR, LGR, HL/BL, PP/BL
f_2	0.358	−0.216	−0.044	BW/BL, PAL/BL, PD/BL
f_3	−0.055	0.036	0.748*1	AF, VN

*1 Significant at 1% level.
*2 Significant at 5% level.

the number of gill rakers, the connection between characters is complex, and it seems as if each character's own unique changes are shown.

Contraction of variation by factor analysis. In order to grasp in a simple form the connection between multiple characters and environmental elements regarding the variation among populations, an analysis by factor analysis was done. The characters used in the analysis were initial growth (IGR) and nine morphological characters (AF, VN, UGR, LGR, BW/BL, PAL/BL, HL/BL, PD/BL, PP/BL)[2] judged to have significant variations among the populations. For BW/BL in which a difference between the sexes was discerned, for convenience an adjusted mean lumping both sexes together has been used.

As a result of calculating the eigenvalues of correlation matrix R by principal component analysis, the number of eigenvalues greater than 1 in value turned out to be three, suggesting the effect of factors in three directions (contribution rate 83.3%) relative to the variation in characters (Table 2). Deducing the factor loadings by the principal factor method using a commonality of 1, the factor loading matrix after rotating the factor axis by the varimax standard is shown in Table 3.

Looking at the relationship between factors and characters from the values of the factor loadings, Factor 1 (f_1) shows a positive correlation with UGR, LGR, HL/BL, PP/BL and a negative correlation with initial growth. Factor 2 (f_2) shows a positive correlation with PAL/BL and PD/BL and a negative correlation with BW/BL. Factor 3 (f_3) shows a positive correlation with AF and a negative correlation with VN.

Looking at the factor scores (Table 4) and the rank correlation coefficients between the factor scores and the latitude, salinity and water temperature of the spawning grounds (Table 5), f_1 which is strongly related to UGR, LGR, PP/BL and initial growth, has a high factor score at Gizhiga Bay and Karaginski and a low score at Obuchi Marsh and Yudo Marsh. In general, the higher the latitude of a population is, the higher tends to be the score and the clearer is the relationship with latitude and water temperature. Factor f_2 which is strongly related to BW/BL, PAL/BL and PD/BL, has a high score at Saroma Lake and Karaginski and a low score at Yudo Marsh, Atsuta and Furen Lake. This factor has a low correlation with the latitude, salinity and water temperature of the spawning grounds. Factor f_3 which is strongly related to AF and VN, has a high score at Saroma Lake and a low score at Obuchi Marsh and Karaginski. This factor has a low correlation with both latitude and salinity but indicates a significant negative correlation with water temperature. A relationship corresponding between environmental element and factor can be clearly discerned between latitude and f_1, but water temperature is related to both f_1 and f_3 so the correspondence is not necessarily singular in meaning.

Discussion

Causes of morphological variation. The nine morphological characters described in detail in the results indicate variations that are statistically significant[2] and peculiar to the habitat (Fig. 1). As the causes of these morphological variations, many environmental conditions[5] such as water temperature, salinity, water quality and feed have been pointed out, but in this study the relationships between the characters and latitude, salinity and water temperature were examined. In the results it was learned that the variations of six characters, IGR, VN, UGR, LGR, HL/BL, PD/BL, indicate strong correlations with the latitude and water temperature of the spawning grounds (Table 1). From the fact that among them are included characters[6] with a strong connection

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to body growth rate like initial growth or HL/BL, it suggests that the variations in this direction are caused by differences in body length among populations with water temperature acting as the medium. On the other hand, the fact that the salinity of the spawning grounds did not indicate a strong connection with any of the characters is thought to be due to the fact that the range of change in salinity in the environments in which the populations have been placed is comparatively narrower than the physiological limits.[7] As for the characters (AF, BW/BL, PAL/BL, PP/BL) in which no connection was discerned with any of these three elements, no correspondence with the environment can be specified.

As Parrish and Saville[8] have pointed out, the variation in terms of phenotype among populations of fishes is governed by both environment and genetics. Barlow[9] stressed that many of the morphological variations of fishes parallel genetic variations. In the populations taken up in this study, a number of variations physiologically and ecologically other than the morphological variations described in the section on results have also been reported. For example, in the Atsuta population a high frequency of hermaphroditic individuals occurs,[1] while the Notoro Lake population has a lacustrine life form,[17] giving them markedly different characteristics compared to other populations. Variations similar to this have been pointed out by Alderdice and Velsen[7] and IIZUKA et al.[10] as well. Also, KOBAYASHI[11] reported that, judging from the IDH isozyme composition, there is a genetic variation between two groups of the Atsuta population which differ in spawning season.

Adding such information to the morphological variations discerned in this study and judging things collectively, the series of variations seen among herring populations has a strong possibility of being strongly dominated by genetic variations. The morphological variations analyzed in this study are a partial reflection of the genetic variations that dominate further at the root. For example, factor f_2 which does not indicate any connection with the environmental

conditions taken up, or the characters (AF, PAL/BL, PP/BL) in which the variations among populations around Japan are greater than the variations between populations around Japan and in the northern waters, might be said to be direct examples of that. Genetic verification of these variational characters is hoped for in future research. (445)

Ecological function of regional populations. The herring in Far Eastern waters live in mutually independent distribution regions, and consist of numerous populations thought to include genetic ramifications. Hubbs[12] says the characteristics of such a self-perpetuating propagating group lie in an evolutionary function which preserves and hands down the genetic characteristics. Also, according to Pianka[13] and Stearns,[14] the differences in life style based on such important characteristics as life span, initial spawning age and spawned egg count, have an important meaning in terms of the adaptational strategy of populations. As KANNO[15] previously pointed out in an analysis of the fluctuation in catch of herring in Notoro Lake, the early spawning - short life span form of life style common in the populations around Japan, as compared to the late spawning - long life span form of life style of pelagic herring typified by the herring in northern waters, is not suited to quantitative expansion, but against severe environmental changes, is thought to have been a favourable adaptational form for survival.[16] Conversely to this, the life style of the pelagic form which is extremely important quantitatively cannot be said to necessarily be a stable life style in the fringe areas of distribution of herring such as around Japan, and this fact is thought to be the cause for the herring of pelagic form to be maldistributed in northern waters. The Sakhalin - Hokkaido line of herring which manifested a big decline in the 1930s is thought to have ramified from localized herring such as of the lentic form and be a rare example that adapted to the environment,[17] which might have made it a genealogical group that would have difficulty in sustaining quantitative prosperity over a long term in the

fringe areas of distribution. When looked at as a whole, the significance of the polymorphic populations which have their respectively unique life styles in Far Eastern waters and maintain an adaptational relationship with the regional environment, is thought firstly to lie in the point that they disperse the risk of species dying out due to environmental change, and secondly to be to function as a seedbed that preserves regional populations which have differing genetic characteristics and gives birth to new and favourable life styles.

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